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Asynchrony of actuarial and reproductive senescence: a lesson from an indeterminate grower

Hugo Cayuela[1], Jean-François Lemaître[2], Lorenzo Rugiero[3], Massimo Capula[4], Luca Luiselli[3,5,6]

[1]Département de Biologie, Institut de Biologie Intégrative et des Systèmes (IBIS), Université Laval, Pavillon Charles-Eugène-Marchand, Québec, QC G1V 0A6, Canada

[2]Université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France

[3]Institute for Development, Ecology, Conservation and Cooperation, via G. Tomasi di Lampedusa 33, I-00144 Rome, Italy

[4] Museo Civico di Zoologia, Rome, Italy

[5]Department of Applied and Environmental Biology, Rivers State University of Science and Technology, P.M.B. 5080 Nkpolu, Port Harcourt, Rivers State, Nigeria

[6]University of Lomé, Faculty of Sciences, Department of Zoology, BP: 6057 Lome Togo

Running head: **Senescence in an indeterminate grower**

Abstract

Aging evolutionary theories predict that patterns of actuarial and reproductive senescence should be aligned, with a common onset of senescence set at the age of first reproduction. However, a few empirical studies reported asynchrony between actuarial and reproductive senescence. This asynchrony is expected to be particularly pronounced in organisms with indeterminate growth. Yet, this process is still poorly documented due to the lack of long-term demographic data on known-aged individuals. We investigated the asynchrony of actuarial and reproductive senescence in the

Introduction

Although a few studies have challenged the idea of an inevitable senescence in nature (e.g. Martinez 1998, Cayuela et al. 2020), it is now broadly recognized that senescence, the decline in the contribution to fitness with increasing age, is a widespread phenomenon across the animal kingdom (Nussey et al. 2013; Gaillard & Lemaître 2020). Senescence can be due to an age-specific decrease in survival probabilities (i.e., actuarial senescence) and/or reproductive performance (i.e., reproductive senescence), two processes usually anchored in the same theoretical framework (Gaillard & Lemaître 2017). Evolutionary theories predict that patterns of actuarial and reproductive senescence should be aligned (Williams 1957, Maynard-Smith 1962), with a common onset of senescence at the age of first reproduction (Williams 1957). However, few recent studies, performed in both laboratory and free-ranging conditions, reported asynchrony between actuarial and reproductive senescence patterns (reviewed in Gaillard & Lemaître 2017). The factors modulating the degree of synchrony are still poorly understood.

The asynchrony between actuarial and reproductive senescence could be particularly pronounced in organisms with indeterminate (i.e., continuous) growth (e.g., fishes, amphibians, and reptiles) where survival and reproductive traits (e.g., fecundity, offspring survival) are often positively correlated with maternal body size, and thus indirectly determined by female age (Hoekstra at al. 2020). This asynchrony could result from non-linear relationships between fitness components and age. The fecundity of females with indeterminate growth recurrently increases with body size and age in a linear way (e.g., in reptiles, Jenkins et al. 2009, Setser et al. 2010, Rose et al. 2018), whereas the strength and the form of the relationship between mortality and age after sexual maturity can be highly variable among species (Colchero et al. 2019, Cayuela et al. 2019a) and populations (Cayuela et al. 2020).

To date, the asynchrony of actuarial and reproductive senescence in indeterminate growers is still poorly documented, mainly due to the lack of long-term demographic data on known-aged

day lasting from 0800 to 1800), by two or three people who searched intensively for snakes in the dilapidated building and neighbouring area of about 100× 80 m. Snakes were captured by hand, and individually marked by ventral scale clipping for future identification. At their first capture, female snakes were measured for snout-vent-length (SVL). We did not measure them on further captures to minimize disturbance and hence risks of their departure from the nesting area, as permanent emigration would bias capture-recapture inferences. We were able to assess the age of 16 females that were captured at juvenile stage over the capture-recapture survey. Detailed information about the number of captures performed each year is given in **Table S1**.

Several females (N = 16) on their first capture were palpated in the abdomen to verify their pregnancy status and to count the number of eggs (Filippi et al. 2007). We also captured 44 additional females in the surroundings of the study area to increase the number of observations of egg clutch size (N = 60 in total).

Reproductive senescence: assessing age-dependent variation in clutch size

First, we verified that SVL was a good proxy of female age by quantifying the correlation between age and SVL in a small set of females for which the age was known (N = 16). Then, we examined how annual egg clutch size was associated with SVL in a larger sample of females (N = 60). In both cases, we used regression models where SVL or egg clutch size were included as the response variable and body size or age were included as explanatory variables. We compared null (i.e. without covariate), linear, and polynomial models using their AIC. We graphically verified the fit of the model by examining model residuals. The analyses were conducted in R program (R Development Core Team 2018).

Modeling age-dependent mortality using BaSTA

Reproductive senescence pattern

Our results confirmed that female SVL linearly increased with age (**Fig.1A** and **Table S2** for model selection procedure) and was thus a robust proxy of their age (R^2 = 0.43). Next, we showed that annual egg clutch size increased with SVL (**Fig.1B**). Although the polynomial model was close (less than 2 AIC points between the two models), the linear model was selected R^2 (0.74) (**Table S3**). Overall, our analyses highlighted that female annual fecundity increased linearly with SVL and age.

Actuarial senescence pattern

BaSTA models revealed that capture-recapture data were best described by a logistic function without any refinement of the shape (**Table 1**). The cumulative probability of surviving was 0.75 until age six, 0.50 until age seven, and 0.25 until age eight (**Fig.1C**). Furthermore, the model showed a strong positive effect of age on hazard rate (**Fig.1D**), which indicates an early and strong actuarial senescence in *H. viridiflavus*.

Discussion

Using capture-recapture data collected over a 29-year period, we showed that *H. viridiflavus* female did not experience any fecundity loss late in life, suggesting a negligible reproductive senescence. In contrast, they suffered from an early and severe actuarial senescence. Taken together, those results revealed a pronounced asynchrony in the senescence process of two main fitness components.

197 general inferences about the ecological and biological factors modulating the asynchrony between
198 aging components. At the intraspecific level, abiotic factors such as temperature and habitat
199 predictability regulate lifespan and actuarial senescence (Sears 2005, Hjernquist et al. 2012, Zhang
200 et al. 2018, Cayuela et al. 2019b), as well as reproductive investment (Morrison et al. 2003, Cayuela
201 et al. 2016, Hughes et al. 2019), in ectotherm vertebrates with an indeterminate growth, which could
202 ultimately modify the asynchrony of senescence patterns. In our study system, the low abundance
203 of natural predators compared to other habitats occupied by *H. viridiflavus* (Philippi et al. 2007)
204 could also buffer actuarial senescence by reducing predation-induced mortality late in life, which
205 might lead to intraspecific variation in the degree of asynchrony between aging components.
206 Furthermore, covariation between mortality patterns and several phenotypic traits of indeterminate
207 growers could result in interspecific variation in the asynchrony of actuarial and reproductive
208 senescence. In particular, the magnitude of the asynchrony could be diminished in species with
209 size-dependent fecundity and negligible or even "negative" actuarial senescence (*sensu* Vaupel et
210 al. 2004, Jones & Vaupel 2017) allowed by high regeneration capacities (e.g., salamanders, Cayuela
211 et al. 2019a), or chemical (e.g., venomous snakes, Cayuela et al. 2019a, Colchero et al. 2019) and
212 armour protection (e.g., turtles, Warner et al. 2016). Overall, our study raises important questions
213 about the ecological and evolutionary mechanisms allowing the uncoupling of reproductive and
214 actuarial senescence processes.
215
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218
219 **References**
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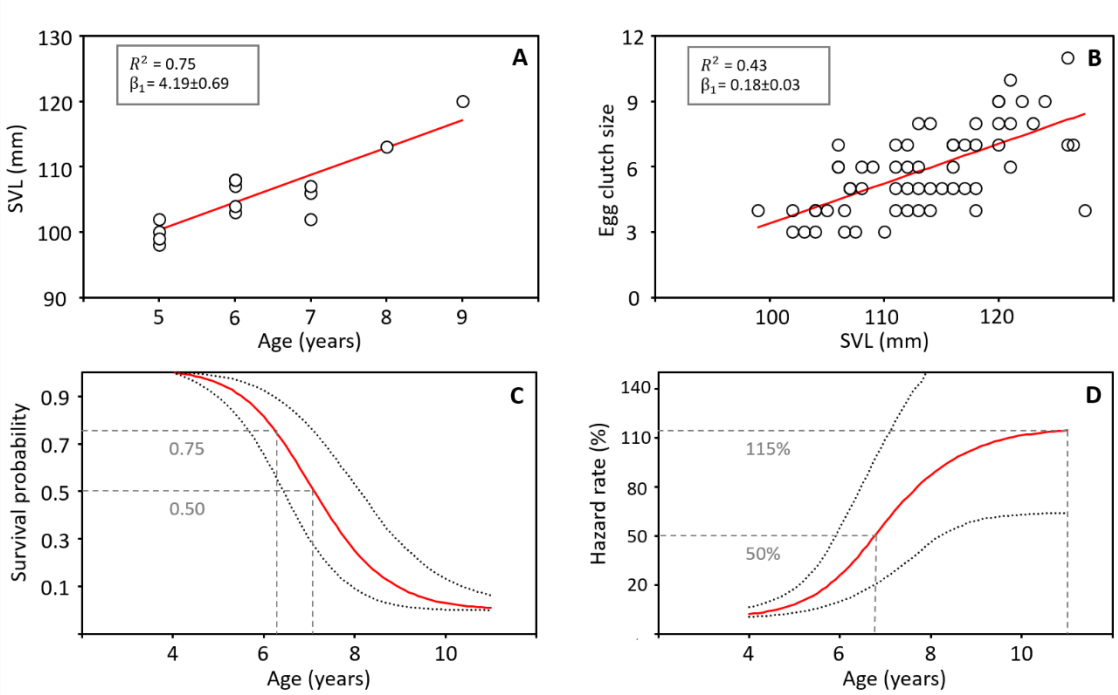

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330 **Fig.1**. Reproductive and actuarial senescence in females of *Hierophis viridiflavus*. (A) Linear
331 relationship between snout-vent-length (SVL) and age. (B) Linear relationship between egg clutch
332 size and SVL. (C) Relationship between survival and age described by a logistic function. (D)
333 Relationship between hazard rate and age described by a logistic function.

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